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Original Article

A Rapid Population Assessment Method for Wild Pigs Using Baited Cameras at 3 Study Sites

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ABSTRACT Reliable and efficient population estimates are a critical need for effective management of invasive wild pigs (*Sus scrofa*). We evaluated the use of 10-day camera grids for rapid population assessment (RPA) of wild pigs at 3 study sites that varied in vegetation communities and wild pig densities. Study areas included Buck Island Ranch, Florida; Tejon Ranch, California; and the Savannah River Site, South Carolina, USA, during 2016–2018. Rapid population assessments grids were composed of baited camera traps spaced approximately 500 or 750 m apart. Two RPA grids were deployed per study site and each grid was deployed twice (4–6 months apart) to assess changes in response to season or population control efforts. We assessed the ability of RPA grids to track population trends, how camera number influenced estimate precision, and how relative abundance indices related to density estimates. We detected changes in occupancy probability, detection probability, and N-mixture estimates following removal operations and between seasons, but the ability of RPA grids to track population trends was dependent on the statistical method used and number of cameras traps. Increasing the number of cameras traps used in RPA grids increased precision, and these results can be used in determining survey design and estimate choice. We found that estimates of occupancy probability, detection probability, and N-mixture estimates were positively correlated with spatially explicit capture–recapture density estimates. Thus, these less labor-intensive estimates from RPA grids showed potential to index the relative abundance of wild pigs in some systems. Our evaluation of RPAs indicates that using study-specific combinations of statistical method and number of cameras can provide a useful tool for monitoring wild pig presence, tracking population trends, and evaluating the effectiveness of management actions. © 2020 The Wildlife Society.

KEY WORDS baiting, camera-trapping, feral swine, rapid population assessments, RPA grid, *Sus scrofa*.

The financial and ecological costs of invasive species make identification and characterization of invasive populations a management priority (Wilcove et al. 1998, Pimentel et al. 2005). Ideally, methods for estimating invasive species' population size should be rapid, cost-effective and efficient, practical to use in field conditions, sensitive enough to detect population trends, and employ statistical methods that allow valid comparisons within and among sites (Engeman et al. 2013). A wide variety of methodologies are available to

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monitor invasive populations, but their applicability depends on the time and labor required, management goals, and characteristics of the target species.

Invasive wild pigs (*Sus scrofa*, aka, feral hogs, feral swine; hereafter referred to as wild pigs) have established populations around the world where they have been introduced (Lewis et al. 2017) as result of their generalist diet (Ballari and Barrios-García 2014), wide niche breadth (Vazquez 2006), high reproductive potential (Taylor et al. 1998), close association with humans as livestock, and value as a huntable species (Mayer and Brisbin 2008, Tabak et al. 2017). Wild pigs pose an economic and ecological risk to invaded systems (Barrios-García and Ballari 2012, Miller et al. 2017) and, because of their expanding range and potential for further expansion, more effective management strategies are critical (Corn and Jordan 2017, Lewis et al. 2017, Snow et al. 2017). Rapid estimates of population trends and early detection of new populations would aid wild pig management decisions by informing the site selection process for control operations as well as monitor effectiveness of management actions. Yet, reliable estimates of wild pig populations remain one of the greatest needs for wild pig management (Choquenot et al. 1996, Seward et al. 2004, Engeman et al. 2013, Beasley et al. 2018).

Density and abundance are common parameters estimated for monitoring wildlife and invasive animal populations. However, they can require significant investment of time and money (e.g., often requiring mark–recapture methods; Keiter et al. 2017, Jiménez et al. 2018), which is challenging if the management goal is to rapidly and cost-effectively survey areas. For many wildlife managers, density and abundance estimates are costly and logistically prohibitive, requiring less labor-intensive estimates be utilized. An efficient method for monitoring populations is to use removal models (e.g., Davis et al. 2016, 2018) because they can provide estimates of abundance reduction using only records of management activities (no. of animals removed and time to remove them). However, removal models can be sensitive to variation in detection probability (which is common in trapping data; Keiter et al. 2017), and it can be challenging to estimate management effort (time investment in searching) when trapping designs are sporadic rather than regularly spaced (Davis et al. 2017).

To address limitations associated with density and abundance estimates, indices have been used to estimate relative abundance of wild pigs and these relative measures can be positively related to pig damage and abundance (Hone 1995, Franzetti et al. 2012, Massei et al. 2018). However, the usefulness of relative abundance indices is limited to site- and season- specific comparisons, and their application has been criticized on the grounds that indices do not always accurately reflect abundance (Jennelle et al. 2002, Karanth et al. 2003, Sollmann et al. 2013). Models that account for imperfect detection using detection–nondetection or repeated count data can be appropriate to use as a surrogate for abundance in some systems, although their utility as a surrogate for abundance has not been assessed for wild pigs (Royle and Nichols 2003, Mackenzie and Nichols 2004, Royle 2004, MacKenzie et al. 2017, Barker et al. 2018).

Camera traps are a noninvasive method that is increasingly being used to monitor wildlife populations and can be used to estimate density, abundance, and relative abundance indices (Burton et al. 2015). By adjusting deployment periods, number of cameras traps deployed, and distance between sampling sites, researchers may also obtain data to address a number of questions about the target population's demographics and habitat use. The minimum duration of surveys varies inversely with the capture rate of the target species, meaning rapid population assessments require high capture rates to achieve accurate and precise estimates (MacKenzie and Royle 2005, Maffei et al. 2011, Guillera-Arroita and Lahoz-Monfort 2012, Shannon et al. 2014). Increased capture rates can be achieved via attractants, such as bait or scent, to encourage animals to visit camera sites (Gerber et al. 2012, du Preez et al. 2014). The number of camera sites is determined by balancing the need for accuracy and precision in population estimates with the costs and logistics of camera deployment (MacKenzie and Royle 2005, Meek et al. 2014). Lastly, the distance between camera sites determines the spatial independence of observations and total area surveyed, and has a direct effect on population estimates (Tobler and Powell 2013). The utility of camera traps offers researchers increased opportunities to rapidly and efficiently monitor wild pig populations (Davis et al. 2018); yet no consistent method has been established that considers these study design factors (but see Keiter et al. 2017).

We evaluated use of baited camera trap grids for rapid population assessment (RPA) of wild pig population parameters at 3 study areas with varying wild pig densities and vegetation communities in Florida, California, and South Carolina, USA. We tested the expectation that RPA surveys could detect population trends and predicted a decrease in population estimates after management or seasonally. We also evaluated 1) the applicability of RPAs by comparing how population estimates varied with density across camera surveys, and 2) how number of cameras influenced the robustness of population estimates. We predicted that variation in population estimates would correlate positively with differences in wild pig density. Increasing the number of cameras was expected to reduce variation in estimates and, therefore, provide guidance on the number of cameras required to produce acceptable levels of error.

STUDY AREA

We selected 3 study areas with varying wild pig densities and vegetation communities to conduct this research. Buck Island Ranch was a 4,250-ha working cattle (*Bos taurus*) ranch located in south-central Florida (27°10′N, 81°21′W, elevation = 38–68 m) that also served as a research area for the University of Florida. The ranch had a subtropical climate and averaged approximately 1,300 mm of annual rainfall with distinct wet (May–Oct) and dry (Nov–Apr) seasons. Average temperatures ranged from 26° C in July to 13° C in January (Boughton and Boughton 2014). The ranch was composed of improved bahiagrass (*Paspalum notatum*) pastures and poorly drained pastures dominated by native C4 grasses interspersed with live oak (*Quercus virginiana*) and cabbage palms (*Sabal palmetto*) hammocks (Vince et al. 1989). The property contained >600 ephemeral wetlands and an extensive network of drainage ditches. For further site description see Boughton and Boughton (2014).

Our California study site encompassed the Tejon Ranch (35°01′N, 118°44′W, elevation = 500–1,950 m). Tejon ranch was a 109,265-ha working cattle ranch located in southern California. The ranch was characterized by a Mediterranean climate, with average annual rainfall of 164 mm that primarily occurred between October and May. Climate across the ranch was variable as a result of the elevation gradient, but average temperatures ranged from 23° C in July to 6.8° C in January at ranch headquarters in Lebec, California (Western Regional Climate Center 2018, station 044863). The ranch had a high diversity of vegetation communities due to its complex terrain, large size, and position within 4 major ecological regions (Great Central Valley, Sierra Nevada, Mojave Desert, and Southwestern California).

Our South Carolina site encompassed the U.S. Department of Energy's Savannah River Site (SRS). The SRS consisted of a 78,000-ha facility bordering the Savannah River in South Carolina (33°20′N, 81°44′W, elevation = 20–130 m). The climate of the SRS was classified as humid subtropical with precipitation distributed evenly throughout the year and averaged ~1,200 mm annually. Average temperatures ranged from 26.7° C in July to 1.7° C in January (Imm and McLeod 2005). The SRS was primarily composed of upland pine interspersed with riparian bottomland hardwood and swamp (Imm and McLeod 2005).

METHODS

We deployed camera girds at each study area to monitor changes in wild pig populations due to removal operations or seasonal variation in grid usage. At Buck Island Ranch, 2 removal operations conducted by University of Florida personnel occurred on either side of a major canal that is known to act as a barrier and thus restricted wild pig dispersal between the north and south portion of the ranch (R. Boughton, University of Florida, unpublished data). During the first removal event, in September and October of 2016, 101 wild pigs were removed from the southern portion of the site. The U.S. Department of Agriculture—Animal and Plant Health Inspection Service (USDA-APHIS) personnel placed a 10-camera baited grid immediately before (Aug 2016) and after (Nov 2016) the first removal, which we referred to as the "south" grid (Table 1; Fig. 1a). A second removal effort, in the northern portion, occurred from December 2017 through February 2018 and removed 252 wild pigs. For the second removal, personnel placed a 20-camera baited grid before (Dec 2017) and after (Feb 2018); we referred to this as the "north" grid (Table 1; Fig. 1a). All activities occurred under University of Florida Institutional Care and Use Committee (IACUC) approved protocols (#201408495 and #201808495).

At Tejon Ranch, we deployed cameras to monitor seasonal changes in wild pig populations. We placed 2 baited camera grids ($n = 10$, referred to as "west" and "east" grids) at Tejon Ranch in August 2016 and February 2017 during the summer and winter seasons (Table 1). Camera grids differed in elevation and vegetation communities, with the west grid being lower in elevation (~1,450 m) in an open, oak savanna community (Fig. 1b). The east grid was higher in elevation (~1,900 m) and in more densely forested oak woodland community. U.S. Department of Agriculture-APHIS personnel conducted field work in California under a protocol approved by the USDA-APHIS and Wildlife Services National Wildlife Research Center's IACUC (QA-2521).

At the Savannah River Site, we evaluated 2 study areas before and after control operations. The first area, referred to as "landfill," included the 120-ha Three Rivers Solid Waste Authority Regional Landfill and surrounding habitat (Table 1; Fig. 1c). The landfill was unfenced and wild pigs were known to utilize this resource. At the landfill, University of Georgia and U.S. Forest Service personnel removed 79 wild pigs in May and June of 2016 and deployed a camera grid ($n = 42$) before (Mar 2016) and after (Aug 2016) the removal event (Table 1). A second site, referred to as "natural" was expected to have lower densities than the landfill site (Table 1; Fig. 1d). At the natural site, personnel removed 21 pigs in June of 2016 and deployed a camera grid ($n = 55$) in April and September of 2016. Camera deployments and wild pig removals occurred under approved University of Georgia IACUC protocol A2015 12-017-Y3-A6.

Rapid Population Assessment Grid Design

Rapid population assessment grids were composed of infra-red (FL and CA) and white-flash (SC) camera traps (RECONYX Hyperfire, Holman, WI, USA) that were deployed for 10 consecutive days. At all sites, personnel placed

Table 1. Summary information for rapid population assessment surveys in Florida (FL), California (CA), and South Carolina (SC), USA, during 2016–2018. Information includes the number of cameras deployed (No. cam), trial type, date ranges (Survey 1 and Survey 2), number of wild pigs removed if applicable (No. removed), approximate distance between cameras sites (Spacing), statistical methods (Methods). Statistical methods include occupancy models (Occu.), N-mixture (N-Mix.), and spatially explicit capture–recapture (SECR).

Site	Grid	No. cam.	Trial type	Survey 1	Survey 2	No. removed	Spacing (m)	Methods
FL	South	10	Removal	Sep 2016	Nov 2016	101	500	Occu., N-Mix
	North	20	Removal	Nov 2017	Feb 2018	252	500	Occu., N-Mix
CA	West	10	Seasonal	Aug 2016	Feb 2017		500	Occu., N-Mix
	East	10	Seasonal	Aug 2016	Feb 2017		500	Occu., N-Mix
SC	Landfill	42	Removal	Mar 2016	Aug 2016	79	750	Occu., N-Mix, SECR
	Natural	55	Removal	Apr 2016	Sep 2016	21	750	Occu., N-Mix, SECR

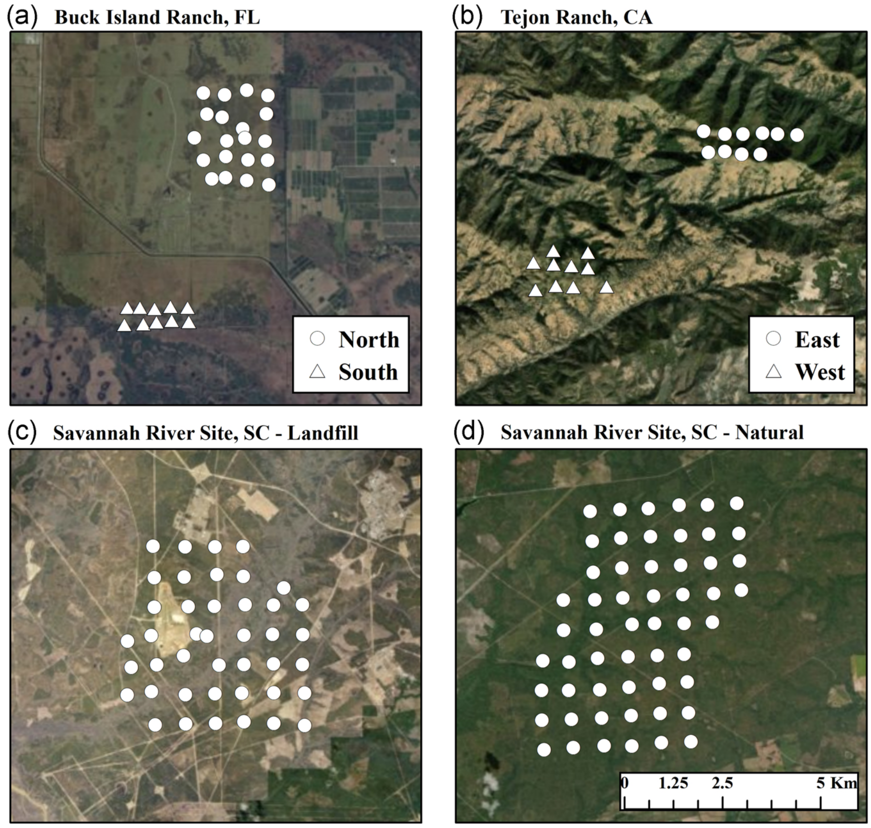

Figure 1. Rapid population assessment grids were deployed at Buck Island Ranch, Florida (1a); Tejon Ranch, California (1b); and the Savannah River Site, South Carolina (1c and 1d), USA. At all sites, 2 camera grids were set either before (South = Aug 2016; North = Dec 2017; Landfill = Mar 2016; Natural = Apr 2016) and after (South = Nov 2016; North = Mar 2018; Landfill = Aug 2016; Natural = Sep 2016) wild pig control operations in Florida and South Carolina or seasonally (Summer = Aug 2016; Winter = Feb 2017) in California. Cameras were approximately 750 m apart in South Carolina and 500 m apart in California and Florida.

cameras on steel t-posts approximately 1 m off the ground and directed them at 12 kg of whole kernel corn (*Zea mays*) placed on the ground 3–4 m away (Fig. 2). Revisits by wild pigs were encouraged by the additional placement of a plastic 5-gallon bucket attached to a t-post and filled with corn in Florida and California (Fig. 2a), a corn-filled plastic pipe with holes to slowly release corn in California (Fig. 2b), or 12 kg of corn on day 5 in South Carolina (Fig. 2c). Personnel placed cameras within 75 m of the center of 500 m (FL and CA) or 750 m (SC) grids in areas expected to encourage pig detection (e.g., near game trails or wild pig sign) and avoid standing water (Cusack et al. 2015). Grids size differed because of differences in protocols between USDA-APHIS and University of Georgia. Cameras in Florida and California systematically took a series of 3 photos every 15 minutes throughout the day. We adopted a 15-minute schedule to balance the expectation that wild pigs would spend extended periods at baited stations with photo processing resources. Camera traps in South Carolina were motion-activated, taking a series of 3 photos/trigger followed by a 1-minute quiet period to allow for repeated detections, which increased the probability of individual identification.

Wild Pig Handling

At all study areas, wild pigs were captured, immobilized, and experimentally marked following IACUC approved protocols. To aid in identification of wild pigs in camera trap images, capture personnel attached ear tags (Y-TEX, Cody, WY, USA) to both ears and collared some individuals with a Global Positioning System device. Marked individuals composed a limited portion of the population, and we used experimental marks in combination with natural marks (pelage and scars) to create population estimates.

Population Estimates from Rapid Population Assessment Grids

At all 3 study areas, we used photos from RPA grids to develop population estimates for wild pigs using occupancy models (MacKenzie et al. 2017) in the package "RMark" (Laake and Rexstad 2008) and N-mixture models via the package "unmarked" (Fiske and Chandler 2011). Additionally, we derived density estimates from spatially explicit capture–recapture (SECR) models in South Carolina because the population contained naturally or artificially marked individuals that could be reliably identified. We estimated density using package "secr" and conducted all analyses in Program R (Efford 2015, R Core Team 2018).

Photos were split into 24-hour periods starting at 1200 over the 10-day trial period. Within these 10 periods, we recorded the number of individuals that visited sites. Individuals sometimes visited the same camera trap multiple times within a 24-hour period and animals that could not be uniquely

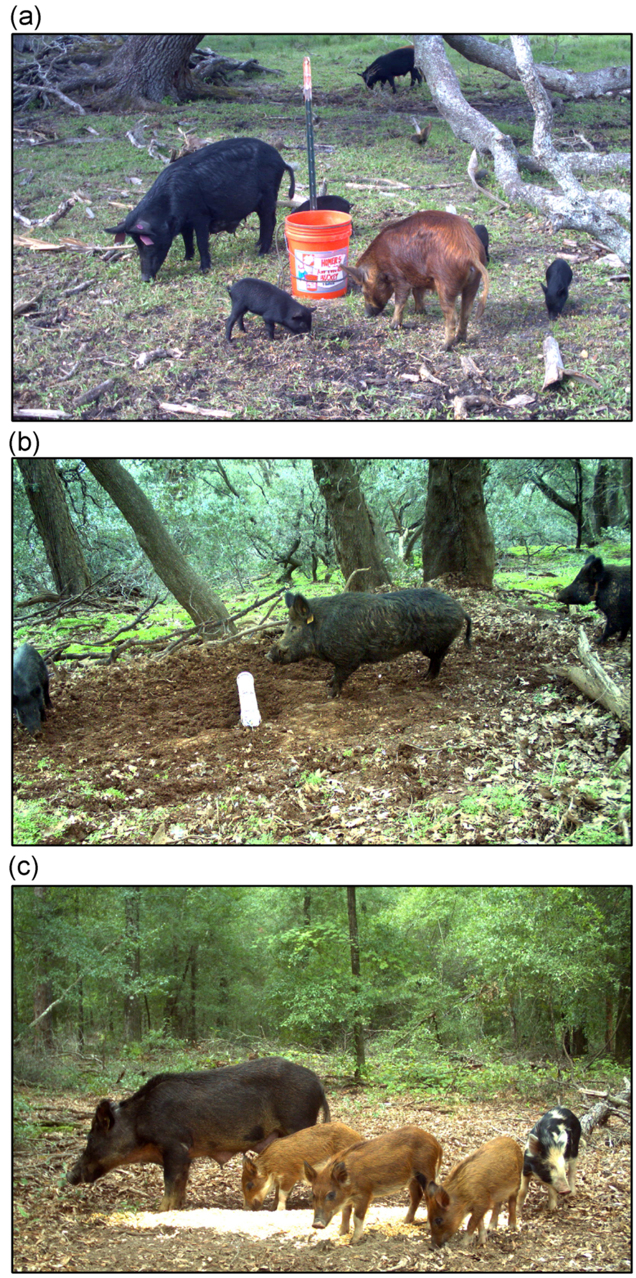

Figure 2. Rapid population assessment (RPA) camera sites were baited with approximately 12 kg of corn that was placed on the ground approximately 3–4 m in front of a camera trap. Revisits by wild pigs were encouraged by the additional placement of a plastic bucket attached to a t-post and filled with corn in Buck Island Ranch, Florida and Tejon Ranch, California (a), USA, or a corn-filled plastic pipe with holes to release corn in California (b), or approximately 12 kg of corn on day 5 at the Savannah River Site, South Carolina (c), USA, during 2016–2018.

identified based on a combination of ear tags, pelage, age, sex, association with other uniquely marked animals, or physical characteristics (e.g., scars), were recorded once to reduce the likelihood of double-counting animals.

We used detection or nondetection data to estimate occupancy and detection probability using occupancy models. Occupancy models, which do not require individual identification, have been proposed as a surrogate for abundance and provide 2 measures of site use (MacKenzie and Nichols 2004, MacKenzie et al. 2017). Detection probability can be related to the intensity of use at a site (Royle and Nichols 2003, Royle et al. 2005), and occupancy probability can be used to evaluate relative use of a site (e.g., Davis et al. 2018). We used single-species single-season occupancy models to estimate occupancy and detection probability (MacKenzie et al. 2017).

N-mixture models used repeated count data and required individual identification of visiting animals at each camera within an occasion (Royle 2004). When interpreting results from N-mixture models, we followed the recommendation by Barker et al. (2018) to present N-mixture results as per camera estimates of relative abundance. N-mixture model estimates can be sensitive to low sample size and we did not include in the results any models that did not converge (Duarte et al. 2018).

Although wild pigs can lack individually identifiable marks in many populations, wild pigs in South Carolina had a large proportion of individuals with black and white spotted pelage and many red or brown individuals had distinct black spots (Keiter et al. 2017). Therefore, individual identification of all individuals was possible with a combination of natural (pelage, scars) and experimental marks (collar and ear tags). We used these data to estimate density via SECR models (Royle et al. 2014). Density estimates included all individuals, regardless of age class, to directly compare with occupancy and N-mixture models. Following recommendations by Efford (2019), we estimated density using an exponential detection function and a habitat buffer wide enough to produce stable density estimates ($4 \times$ initialsigma).

Evaluating Effects of Camera Number

To evaluate how the number of camera traps influenced population estimates, we used data from South Carolina, which consisted of a greater number of camera sites. At both the landfill and natural areas we estimated occupancy probability, detection probability, and N-mixture estimates from a group of randomly selected cameras taken from the total number of sites on each grid. Therefore, variation in camera trap number resulted in changes in trap density within the total grid. The number of camera traps used to create estimates ranged from 5 to the total for that grid minus one, and we calculated estimates for 1,000 bootstrapped iterations of each camera sample size. To estimate how increasing camera number influenced the precision of estimates, we calculated the coefficient of variation (CV) for occupancy probability, detection probability, and N-mixture estimates across the 1,000 iterations.

RESULTS

Population Trends

We expected occupancy probability, detection probability, and N-mixture estimates to decrease between camera trap surveys as a result of removal operations (FL and SC) or vary as a result of seasonal differences in habitat use (CA). In Florida, occupancy probability was reduced between pre- and postremoval surveys, following expectations (Fig. 3). Wild pigs were present at all camera traps before removals

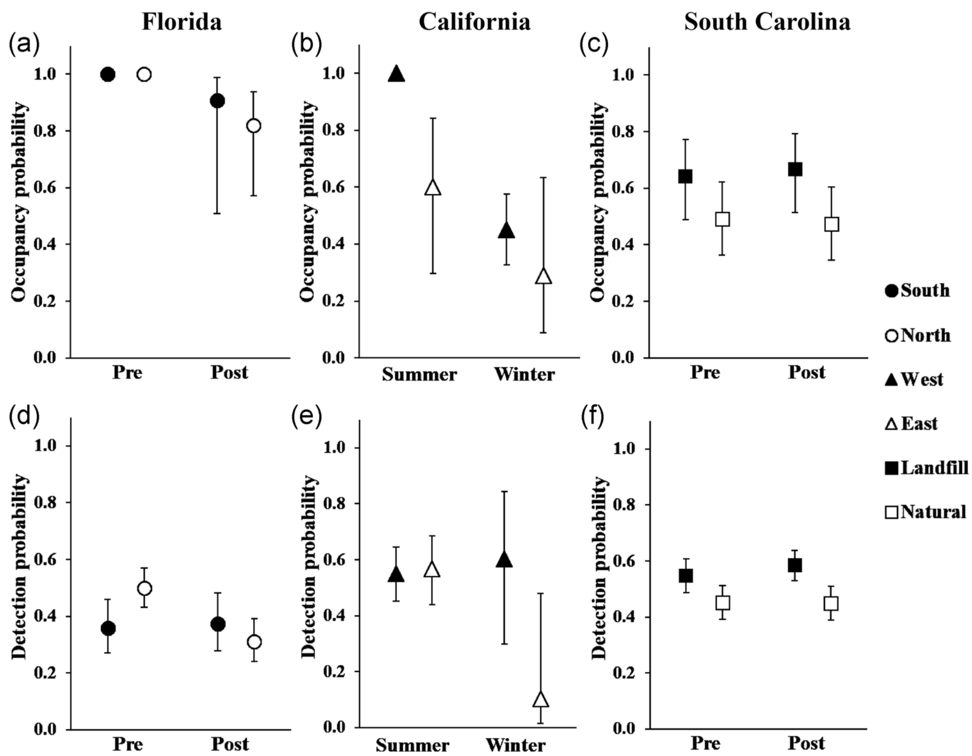

Figure 3. Occupancy and detection probability (±95% CIs) from rapid population assessment grids at Buck Island Ranch, Florida, Tejon Ranch, California, and the Savannah River Site, South Carolina, USA, during 2016–2018. Occupancy and detection probability were estimated before (South = Aug 2016; North = Dec 2017; Landfill = Mar 2016; Natural = Apr 2016) and after (South = Nov 2016; North = Mar 2018; Landfill = Aug 2016; Natural = Sep 2016) control operations in Florida and South Carolina or seasonally (Summer = Aug 2016; Winter = Feb 2017) in California.

(occupancy probability = 1.0), but postremoval occupancy probability estimates were 0.91 (95% CI = 0.51–0.99) for the south grid and 0.82 (95% CI = 0.57–0.94) for the north grid. Detection probabilities did not differ before and after removal operations for the south grid but decreased postremoval for the north grid (Fig. 3). N-mixture estimates did not converge for any surveys in Florida.

In California, all camera traps in the west grid were visited by wild pigs during summer (occupancy probability = 1.0), but occupancy decreased to 0.45 (95% CI = 0.33–0.58) during winter camera surveys. Detection probabilities did not differ between surveys on the west grid, which exhibited wider confidence intervals during winter surveys (Fig. 3). N-mixture estimates did not converge for either survey on the west grid. Occupancy and detection probability estimates in the east grid decreased from summer to winter surveys (Fig. 3). N-mixture model estimates for the east grid were 1.18 (95% CI = 0.63–2.23) individuals/camera in summer and decreased to <1 individual/camera for winter surveys (0.11, 95% = 0.02–0.75).

In South Carolina, the landfill had larger estimates of occupancy and detection probability compared with those at the natural site and estimates at both sites were similar before and after control operations (Fig. 3). N-mixture estimates at the landfill were greater before control (10.60 individuals/camera, 95% CI = 9.27–12.09) relative to after (6.30, 95% CI = 5.47–7.23). A weaker, but similar, effect was observed at the natural site precontrol (4.14, 95% CI = 3.46–4.95) versus postcontrol (3.04, 95% CI = 2.51–3.68).

Relationship of Population Estimates to Density Estimates

Consistent with predictions, occupancy probability, detection probability, and N-mixture estimates were positively related to survey-level variation in density in South Carolina (Fig. 4). Based on results from SECR models, density estimates (individuals/km^2) were unchanged at the landfill (5.05, 95% CI = 4.33–5.90 precontrol; 4.64, 95% CI = 3.90–5.52 postcontrol) and natural site (1.76, 95% CI = 1.42–2.19 precontrol; 1.65, 95% CI = 1.30–2.08 postcontrol), indicating that the management intensity was too low to detect a change in population density by these methods. No response was detected in occupancy or detection probability at either study area, though N-mixture estimates differed at the landfill and similar effect was observed at the natural site.

Effects of Camera Number

Results from the landfill and natural grids in South Carolina indicated that the range and variation of estimates decreased as the number of cameras used increased. At the landfill (Fig. 5) and natural site (Fig. S1, Supporting Information available online), the range and variation in all estimates consistently decreased as camera number increased. N-mixture estimates appeared to be sensitive to lower camera numbers with outliers that greatly increased the range of estimates (Fig. 5e and f).

As expected, the CV decreased as camera number increased. For both the landfill and natural grids in South Carolina, CV values were greater from N-mixture estimates

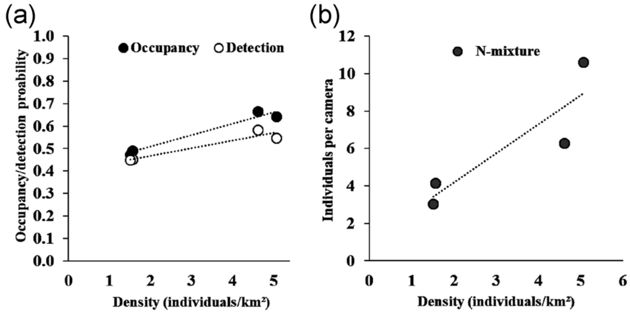

Figure 4. The relationship between different wild pig population estimates created from rapid population assessment grids. Surveys were conducted before (Landfill = Mar 2016; Natural = Apr 2016) and after (Landfill = Aug; Natural = Sep 2016) removal operations at the landfill and natural sites on the Savannah River Site, South Carolina, USA. Occupancy probability and detection probability (a), and N-mixture estimates (b) were compared with density (individuals/km^2) estimated via spatially explicit capture–recapture models.

than occupancy and detection probability (Fig. 6; Fig. S2, Supporting Information). Following an exponential relationship, CV estimates decreased as camera numbers increased. This reduction in variation allowed for a better estimate of error associated with varying camera number for RPA grids (Table S1, Supporting Information). N-mixture estimates required a greater number of cameras than occupancy and detection probability to attain similar CV values (Fig. 6). In addition, the natural grid consistently required a greater number of cameras to attain similar CV values than the landfill (Fig. S2).

DISCUSSION

At all study sites, RPA grids were effective at detecting wild pigs. The statistical approaches we used to track population trends were able to quantify changes in wild pig populations through time and space. Wild pigs were detected within each 10-day survey, demonstrating that this method can provide presence data, which could be critical in identifying recently established populations. In South Carolina, occupancy probability, detection probability, and N-mixture estimates were positively related to SECR density estimates, suggesting these methods have potential to serve as surrogates of abundance or density in systems with similar characteristics, although the relationship between estimates and density requires further examination. Estimate precision increased substantially with the number of camera traps deployed in RPA grids. The ability of RPA grids to track population trends due to removal operations and seasonal differences in habitat use varied depending on the statistical method and, importantly, the number of camera traps used.

Results from RPA grids provided valuable information about the ability to detect population trends and comparability of

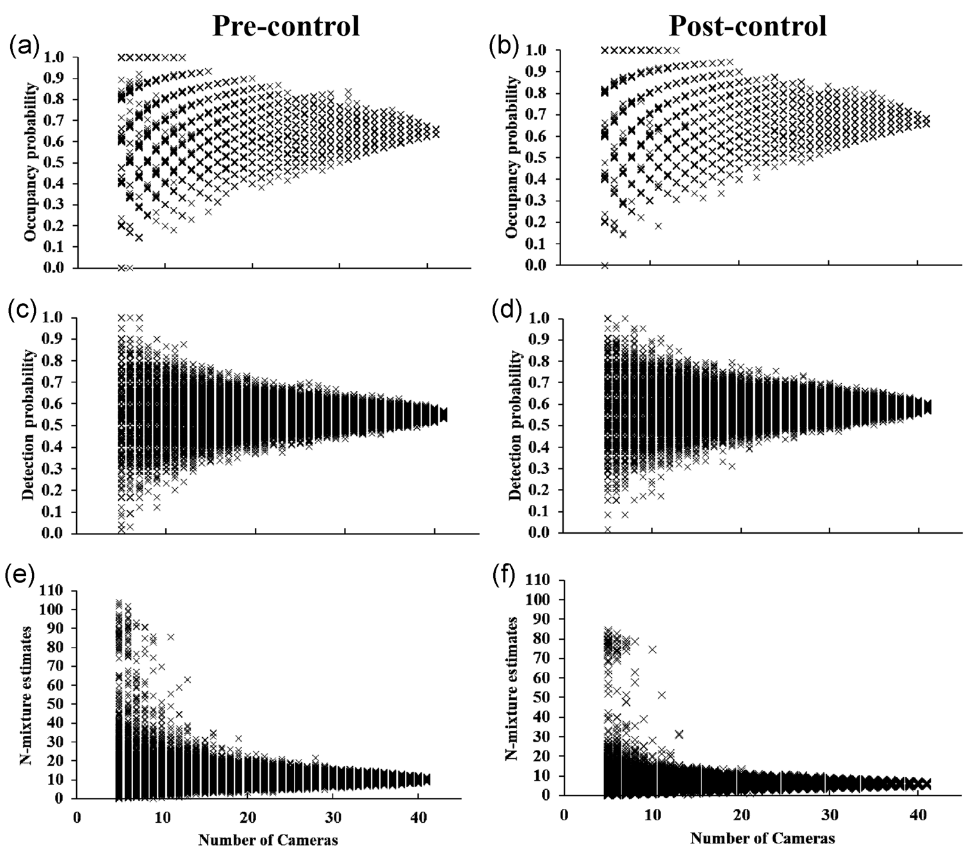

Figure 5. Population estimates of wild pigs at the landfill site on the Savannah River Site, South Carolina, USA. Occupancy probability (a and b), detection probability (c and d), and N-mixture estimates (individuals/camera; e and f) were estimated from 1,000 bootstrapped iterations of 5–41 randomly selected cameras from the total landfill grid. Included are figures from the preremoval (Mar 2016; a, c, and e) and postremoval (Aug 2016; b, d, and f) grids.

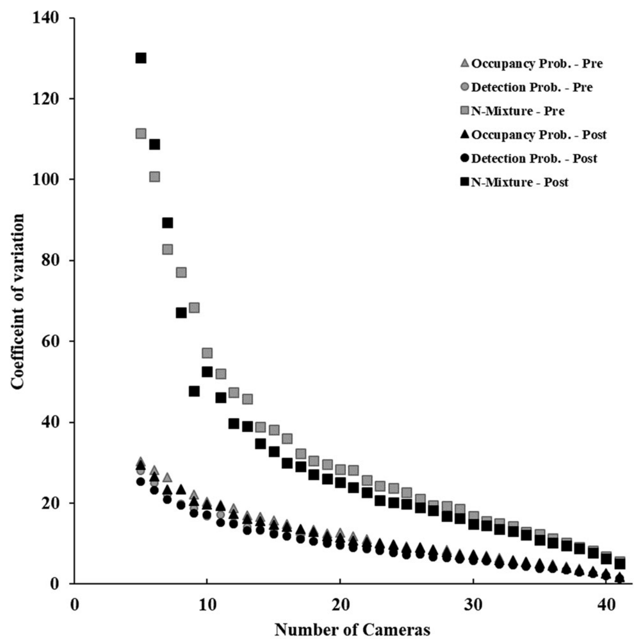

Figure 6. The coefficient of variation in occupancy probability, detection probability, and N-mixture estimates of wild pigs at landfill site on the Savanah River Site, South Carolina, USA. Estimates were produced from 1,000 iterations of randomly selected cameras from the pre- (Mar 2016) and postremoval (Aug 2016) surveys. The number of cameras used to create estimates ranged from 5 to one minus the total number of cameras ($n = 42$).

population estimates to density estimates. Wild pigs were expected to shift their habitat use between seasons in California, and wild pigs were less likely to be detected at high-elevation sites during winter. Reductions were detected in Florida following removal operations but it is unknown how estimates relate to reductions in density. In South Carolina, expected grid-level differences in population size (landfill site > natural site) were detected by occupancy, N-mixture, and SECR models. We detected a positive occupancy–density relationship similar to previous studies (Rovero and Marshall 2009, Tempel and Gutiérrez 2013, Clare et al. 2015, Villette et al. 2015, Linden et al. 2017), but the limited number of study grids, presence of bait, and the gregariousness of wild pigs make our results difficult to compare with previous work on other species.

Requiring further investigation, the relationship between density and both occupancy and detection probability may be less informative for wild pig populations at high densities because of the asymptotic and nonlinear relationship between these parameters (Freckleton et al. 2005, Noon et al. 2012). Wild pigs were attracted to camera sites with bait to increase detection probability, making rapid surveys possible (Gerber et al. 2012, du Preez et al. 2014). Baiting design, however, can influence the spatial behavior of wild pigs, which could inflate occupancy model estimates and make valid comparisons of populations in space and time challenging if individuals in lower density populations are strongly attracted to bait over broad spatial scales (Thorn et al. 2009). N-mixture estimates may be best interpreted as relative measure of abundance (Barker et al. 2018). The correlation between N-mixture estimates and SECR density estimates suggests a positive relationship between these metrics as well. However, the limited number of camera grids evaluated here suggests that further investigations are required to evaluate this relationship. Ultimately, N-mixture models require relatively large sample sizes and individual identification, which might not be achievable in many systems because of similar morphological characteristics of animals (e.g., pelage patterns) and limited field resources. Irrespective of the statistical method used, the utility of RPA grids depends on their ability to characterize wild pig populations and monitor population trends, which varies based on the grid design and number of cameras used.

When deploying RPA grids, a primary field consideration is the distance between camera sites, which can influence independence within an occasion (Royle 2004, MacKenzie et al. 2017). In South Carolina where individual identification was possible, >2 camera sites were visited by the same individual within a single occasion. Although a rare occurrence, this violates the assumption of site independence, which was likely accentuated by the presence of bait. In addition, longer sampling occasions (e.g., >1 day) would likely lead to an increased opportunity for wild pigs to visit multiple baited camera sites within an occasion. Future investigations could evaluate the relationship between camera distance and independence between cameras, which likely varies with home range size and study area characteristics (Schlichting et al. 2016, Garza et al. 2017, Kay et al. 2017). Larger grid sizes are expected to increase spatial independence, yet this also increases the likelihood that animals using areas within the grid could be undetected, which may be important for management and control of wild pig populations.

The number of camera trap sites to maintain in a grid is another key consideration for deploying RPA grids, which can influence the ability to compare population estimates in space and time, as well as the cost and practicality of implementing RPA surveys. Consistent with other studies focused on sample size, the number of camera traps deployed in RPA grids influenced the precision of estimates (MacKenzie et al. 2017). Following predictions, increasing the number of sites (i.e., camera traps) increased precision for all metrics (MacKenzie and Royle 2005, Shannon et al. 2014). However, consistent with the objectives of RPA grids, we tested the reliability of estimates from a relatively small number of camera sites, which might typically be used by field personnel with limited time and resources. In South Carolina, occupancy and detection probability estimates were relatively robust at low camera numbers, compared with N-mixture estimates, suggesting occupancy models are a comparatively efficient method to monitor wild pigs. N-mixture estimates were more sensitive to low camera number, which was likely responsible for the majority of models evaluated for Florida and California not converging. Increased detection probability can decrease the number of cameras required to produce reliable estimates (MacKenzie and Royle 2005, Maffei et al. 2011, Guillera-Arroita and Lahoz-Monfort 2012, Keiter et al. 2017).

Fewer camera traps were required at sites with relatively greater density to attain similar CV values. Ultimately, the number of camera traps that managers decide to use in RPA grids should be determined by the statistical method, study area characteristics, and acceptable level of precision for estimates. In addition, 1-day occasions helped with reliably identifying unique individuals at camera locations; longer sampling occasions (i.e., >1 day) would likely increase the probability of double-counting animals in the systems we evaluated.

Study area and animal attributes should be considered when determining the most appropriate models for evaluating population characteristics. Wild pigs can be identified based on natural marks or color patterns in some systems; but, often, only a subset of the population can be identified using natural marks (Mayer 2009, Keiter et al. 2017, Jiménez et al. 2018). Models, such as N-mixture models, require that animals be uniquely identified. Thus, other methods, such as mark–resight models, might be more appropriate, where a portion of the population is uniquely identified and the remaining animals are unmarked (McClintock and White 2012). Further, we were able to individually identify wild pigs during 1-day occasions in our system while controlling for double-counting individuals; longer occasion lengths (i.e., >1 day) might challenge the ability to differentiate individuals with similar attributes (e.g., age, sex, pelage) in populations that lack natural or artificial marks. Therefore, methods such as occupancy modeling, that do not require individual identification of animals, can be a good alternative to efficiently evaluate population characteristics of a species. In addition, researchers could include site- and season-level covariates to better understand patterns of populations through space and time (MacKenzie et al. 2017, Davis et al. 2018).

MANAGEMENT IMPLICATIONS

Rapid population assessment grids were effective in providing presence and population estimates using multiple statistical methods and add to our understanding of how to monitor management effects. When implementing RPA surveys, our results can be used to develop study designs in new systems that balance camera number with the choice of statistical method and an acceptable precision level of estimates. The rapid and cost-effective nature of RPA grids suggests they can be used at multiple spatial and temporal scales to better understand how wild pig populations relate to levels of ecological and agricultural damage or disease risk by simultaneously tracking wild pig populations, damage, and disease prevalence in an area. This information could be used by managers to predict levels of damage and economic cost based on wild pig population abundance or invasion. At a coarser scale, RPA grids could be a rapid way to track changes in population size, evaluate the effectiveness of management actions, and monitor areas threatened by wild pig invasion, especially when trapping is primarily used for population control, which involves routine camera deployment.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1. Occupancy probability, detection probability and N-mixture estimates of wild pigs at the landfill site on the Savannah River Site, South Carolina, USA, from 1,000 bootstrapped iterations of 5–53 randomly selected cameras from the greater natural grid.

Figure S2. The coefficient of variation in occupancy probability, detection probability, and N-mixture estimates of wild pigs at natural site on the Savanah River Site, South Carolina, USA.

Table S1. The number of cameras required to achieve a range of coefficient of variation values from rapid population assessment RPA grids at the landfill and natural sites on the Savannah River Site, South Carolina, USA.